



How dung beetles respond to a human-modified variegated landscape in Mexican cloud forest: a study of biodiversity integrating ecological and biogeographical perspectives

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ABSTRACT

Aim To analyse how the dung beetles (Scarabaeinae) respond to a modified, variegated landscape, taking into account the biogeographical peculiarities of the Mexican Transition Zone.

Location This study covers cloud forest (CF) of the Sierra Norte de Puebla mountain range and part of the Sierra Madre Oriental mountain range (Mexico).

Methods We applied proportional sampling based on the landscape variegation model with Scarabaeinae as the indicator group, and using two approaches: structural units (vegetation type) and spatial units (windows). We used two measures – richness and Shannon diversity – and applied multiplicative diversity partitioning to obtain independent alpha and beta diversities for the landscape, windows and vegetation types. We grouped species by biogeographical distribution pattern for the biogeographical analysis and by whether they were originally from CF.

Results The transformation of CF into secondary forest, pastures and other types of vegetation increases the Scarabaeinae diversity of the landscape, in vegetation types and windows. This increase is the result of species arriving from the tropical lowlands. However, the original dung beetle community of the CF dominates at different scales in the number of species, abundance and biomass. With increasing habitat modification, beta diversity increases in the windows, and species with the Tropical Palaeoamerican distribution pattern increase in abundance in vegetation types and windows.

Main conclusions The variegated character of the landscape explains well the distribution and diversity of this dung beetle community. The peculiar characteristics of the Mexican Transition Zone have an effect owing to the overlap of fauna with different biogeographical origins. The conversion of fragmented landscapes to variegated landscapes could be a conservation goal in human-modified mountain landscapes. Sampling proportional to the area of different types of vegetation and the use of windows offer an alternative experimental design in variegated landscapes.

Keywords

Biogeographical distribution pattern, conservation, landscape variegation model, Mexican Transition Zone, Scarabaeinae, true diversities.

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INTRODUCTION

Studies in tropical and subtropical regions show that dung beetle (Scarabaeinae) diversity generally decreases with increasing habitat transformation (Nichols *et al.*, 2007; Gardner *et al.*, 2008; Navarrete & Halffter, 2008). However, in cloud forest (CF), this pattern is not as clear. Dung beetle richness in CF is not greater than the number of species recorded for anthropogenic environments when the latter conserve parts of their arboreal cover, and diversity can in fact increase, as found for the shaded coffee plantations in central Veracruz, Mexico (Pineda *et al.*, 2005). In other cases, richness is similar between the forests and modified areas, but species composition is different, as found for the mountains of Colombia (Escobar, 2004) and Peru (Horgan, 2009). In general, richness decreases in pastures and agricultural crops without arboreal cover (Nichols *et al.*, 2007).

Traditionally, studies on the effects of habitat transformation on dung beetle communities have been approached via the patch-matrix-corridor model (e.g. Klein, 1989; Pineda *et al.*, 2005; Quintero & Roslin, 2005; Nichols *et al.*, 2007; Gardner *et al.*, 2008; Navarrete & Halffter, 2008) defined by Forman (1995). An alternative approach is the landscape variegation model proposed by McIntyre & Barrett (1992), which incorporates the idea of continuous and gradual changes to the vegetation cover. The original vegetation type, instead of being destroyed, persists in differently sized areas and states of alteration, and the limits between the landscape elements are difficult to identify (McIntyre & Hobbs, 1999; Manning *et al.*, 2004). The permeability of the edges is determined by the degree of contrast between landscape elements, and in consequence species mobility should be greater in a variegated landscape than it is in a fragmented one with clearly defined edges (McIntyre & Hobbs, 1999; Ewers & Didham, 2006).

Although several authors highlight the importance of species biogeographical affinity when addressing the response of dung beetles to habitat change, few studies take this parameter into account (Nichols *et al.*, 2007; Gardner *et al.*, 2008). Escobar *et al.* (2007), for example, demonstrated that the response of Scarabaeinae to the transformation of forests to pastures along altitudinal gradients is related to the geographical position of the mountain and the biogeographical history of the species. Transformation of the original habitat facilitated the entrance of species that are ecologically and evolutionarily linked to adjacent ecosystems (Halffter *et al.*, 1995; Escobar *et al.*, 2007; Davis & Philips, 2009).

Cloud forest ecosystems are limited in area and are estimated to still cover 1% of the area of Mexico (Rzedowski, 1996; Challenger, 1998). These forests are naturally heterogeneous owing to orographic conditions and climate (e.g. hurricanes, landslides), and have a long history of human land use that dates back to pre-Hispanic times (Challenger, 1998). Another characteristic of CF in the Mexican Transition Zone (MTZ) is the mixed biogeographical origin of its biota, which is comprised of elements of both northern and Neotropical origin. The relative importance of these regions

of origin differs depending on the taxonomic group. For canopy trees and birds, Nearctic species dominate, while for the other plants, vertebrates and arthropods species with a Neotropical affinity dominate (Challenger, 1998). Although for the flora, a high number of species exclusive to CF has been reported (Rzedowski, 1996), for the fauna in general and particularly for dung beetles, the degree of association is much less evident. Additionally, CF appears to be a limited habitat for the Scarabaeinae owing to the scarcity of food, the topographic complexity and the climate (Gaston & Chown, 1999; Escobar *et al.*, 2005; Verdú *et al.*, 2007).

In this study, we used dung beetles – a very useful group of insects for applied studies in biodiversity (Halffter & Favila, 1993; Spector, 2006) – to evaluate the response of the community in a variegated CF landscape. To this end, we used two approaches: a spatial approach where discrete subsamples were chosen from the landscape (referred to hereafter as windows), each with a different degree of CF transformation, and a structural approach using different vegetation types. Specifically, we posed the following questions: (1) How do the diversity, abundance and biomass of Scarabaeinae species vary in a variegated landscape in the MTZ? (2) How different is the dung beetle community of CF from that of other types of vegetation? and (3) What is the biogeographical affinity of the species inhabiting the different windows and vegetation types on this landscape?

METHODS

Study area

The study area is located in the Sierra Norte Mountain Range in the state of Puebla, Mexico (19°55'13"–20°00'13" N, 97°20'23"–97°32'39" W; Fig. 1). In this region, CF grows from 900 m a.s.l. up to 1500 m a.s.l. Lower down it is replaced by medium tropical forest, and higher up there is pine-oak forest. Annual precipitation/temperature ranges from 4134 mm/20 °C at the lower altitudinal range to 3000 mm/> 15 °C at the higher altitudes (García, 1988).

In contrast to other CFs in Mexico that have significantly decreased in size over the last 30 years as a consequence of increasingly intense land use (Cayuela *et al.*, 2006), the study area has suffered few changes at the landscape level, as revealed by a comparison of satellite images from 1973–1979 and 2000–2002. The orography of the study landscape is complex, and its high heterogeneity is a result of both disturbance by humans and natural disturbances; the latter are mostly caused by hurricanes (e.g. hurricane Dean 2007) and landslides (e.g. that of 1999) caused by rainstorms (Lugo-Hubp *et al.*, 2005) and have produced a mosaic of vegetation in different stages of succession. Currently, the landscape is dominated by continuous CF, secondary forest (SF) of different ages, interlaced with coffee plantations, crops, tree plantations, tracts of ferns and pastures (Fig. 1 and Table 1). According to the grouping by McIntyre & Hobbs (1999), our landscape can be defined as variegated because still it has between 60% and 90% of its

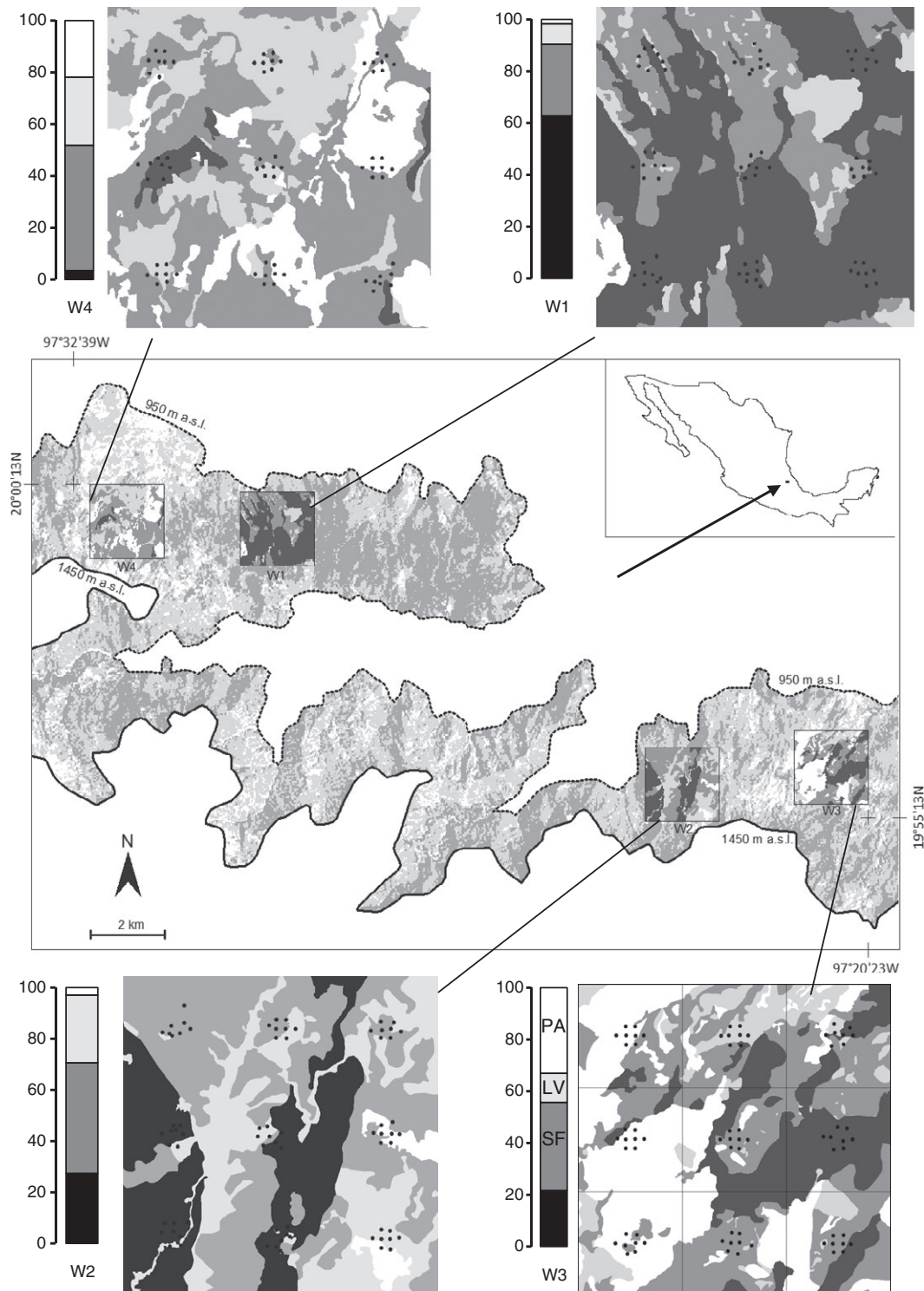


Figure 1 Landscape studied in the Sierra Norte de Puebla mountain range/Mexico between 950 m a.s.l. (dotted line) and 1450 m a.s.l. (solid line). W1–W4 are windows measuring 2×2 km (400 ha) each, and represent $\approx 12\%$ of the area of the whole landscape. Windows are numbered in order of greatest to least cloud forest cover. Points within the windows indicate the location of each trap. W3 exemplifies the cells used to place the traps. Colours within the windows and bars indicate vegetation type (expressed as a proportion of the area of the window) classified according to land use and vegetation structure, and verified using QuickBird satellite images 2006–2008: cloud forest (CF), secondary forest (SF), low vegetation (LV), pasture (PA). Outside of the windows, the classification was based on Landsat satellite images from 2000. Contour lines are from INEGI 2006.

Table 1 Description of the types of vegetation evaluated.

CF (29%)	In different states of conservation, dominated by trees 15–25 m in height, including areas notably disturbed by hurricane Dean in August 2007 ($\approx 10\%$). <i>Matudaea trinervia</i> is the dominant tree species, along with species of <i>Pinus</i> , <i>Liquidambar</i> and <i>Quercus</i> .
SF (38%)	All vegetation dominated by trees > 4 m but < 15 m in height, mostly secondary forest ($\approx 85\%$), including abandoned coffee plantations and fruit orchards ($\approx 10\%$), shaded coffee plantations (< 5%), pine plantations (< 1).
LV (18%)	Vegetation height is < 3 m. Characterized by diverse uses: includes areas markedly disturbed by recent fire, hurricanes, landslides or tree clearing; areas dominated by ferns (W1–3), young pine plantations (W2), corn and bean crops (W4) and unshaded coffee plantations (W4).
PA (15%)	All open vegetation where there is evidence of the recent presence of livestock. Many pastures have large isolated standing trees.

CF, cloud forest; SF, secondary forest; LV, low vegetation; PA, pasture. The percentage of the total area of the pooled windows is given in parenthesis.

original habitat, when CF and SF together are considered to be the original habitat in different stages of modification (Fig. 1, Table 1). As subsamples of the landscape, the windows can also be categorized (compare Lindenmayer *et al.*, 2003): W1 is intact (> 90% original and modified habitat), W2 is variegated, and W3 and W4 are fragmented (10–60%, Fig. 1, see below for delimitation of windows and vegetation types).

Sampling design

Given that it was not possible to delimit, *a priori*, the elements or environments that make up this landscape, we used semi-random sampling. That is, we selected four areas which we called windows (W), measuring 2×2 km (400 ha) each and representing a different CF transformation scenario, with the proportion of CF cover ranging from 62% (W1) to 3% (W4; Fig. 1). Windows were separated by at least 2 km. Trap sites were determined by dividing each window into nine cells of the same size (Fig. 1, W3). Using ARCVIEW 3.3 (ESRI, Redlands, California, USA), we located the centre of each cell and obtained the geographical coordinates of eight sites separated by 50 m arranged in a roughly hexagonal pattern (points in Fig. 1). A distance of 50 m between traps is considered to minimize trap interference (Larsen & Forsyth, 2005).

Once in the field, we used a GPS (*Garmin Etrex Vista*, precision > 4 m) to find the predetermined point and set the trap (eight traps per cell, 72 traps per window, 288 traps in total). For $\approx 5\%$ of all traps, the predetermined point was inaccessible owing to the topography, and an alternative nearby site was used (Fig. 1). Each trap consisted of a container with a 1 L capacity (11.5 cm diameter \times 13.5 cm deep), buried flush with the soil and baited with ≈ 20 g fresh human excrement placed in a 25-mL cup suspended by a wire in the larger container, which was one-fourth full with a solution of water, salt and soap to prevent the beetles from escaping. The results of a pilot study carried out in the study area (July–October 2007) indicated that carrion, which is usually used as a complementary attractant for dung beetle inventory, should not be used owing to its low capture effectiveness.

Sampling was intensive and done in the shortest time possible during the rainy season between 2 June and 23 July 2008 when the dung beetles are most active (Hanski & Cambefort, 1991). Each trap was open for 48 h after which the specimens captured were collected, placed in labelled plastic

bags with 70% alcohol and taken to the laboratory for identification. Beetle biomass was obtained by drying the insects at 40 °C for a week and then weighing them on a digital balance (A&D GX200, $d = 0.001$ g); we weighed all the individuals of a given species caught in each trap. Mean biomass per trap (BT) and mean individual biomass per trap (IBT) were calculated for each window and vegetation type.

At each trap site, we recorded the type of land use and measured canopy cover, tree diameter at breast height, tree height and slope. After sampling, we used QuickBird satellite images (2006–2008) as well as land use and vegetation structure data for the trapping sites to identify the following four vegetation types: CF, SF, low vegetation (LV) and pasture (PA) (Table 1). Heterogeneous in their interior, these vegetation types also differ from each other with respect to several environmental parameters (Table 2).

We carried out proportional sampling (Schoereder *et al.*, 2004) of each vegetation type within each window and for the vegetation types representative of the landscape. A goodness-of-fit analysis revealed that the number of traps used for sampling in each vegetation type did not differ significantly from expected for the windows, vegetation types or landscape (Table 3), that is using semi-random sampling, the sampled vegetation type did not deviate significantly from the proportional representation of each vegetation type.

Data analysis

Under the spatial approach, the sampling units are the four windows, and under the structural approach, the sampling units are the four vegetation types. For each window, the sampling units are the different vegetation types, and for each vegetation type, the sampling units are the same type of vegetation in the different windows (Fig. 1, Table 4). Sampling representativeness in each of the sampling units was evaluated as the percentage of species observed relative to the number of species predicted by two nonparametric abundance-based estimators (ACE, CHAO1) using EstimateS ver. 8.2 (Colwell 2004). We compared the richness of each window and vegetation type with the confidence intervals for the whole landscape (De Vries *et al.*, 1997). To analyse the changes in abundance and biomass between windows and vegetation types, we applied a nonparametric one-way ANOVA (Kruskal–Wallis).

Table 2 Environmental parameters for vegetation types (VT) and Windows (W). The mean, standard deviation and significant differences between VT or W (Kruskal–Wallis test) are given. Windows are listed in order of greatest to least cloud forest cover.

	CF	SF	LV	PA	W1	W2	W3	W4
Canopy cover (%)	82.44	80.13	33.30	17.02	74.97	66.96	52.15	52.78
SD	±9.95	±12.04	±32.37	±28.93	±18.74	±29.42	±40.17	±37.00
<i>P</i> < 0.05	PA, LV	PA, LV	SF, CF	SF, CF	W4	–	–	W1
DBH (cm)	36.22	18.79	4.12	10.33	28.65	20.25	17.72	13.19
SD	±19.91	±8.72	±6.75	±15.82	±22.74	±14.47	±18.97	±12.81
<i>P</i> < 0.05	PA, LV, SF	PA, LV, CF	SF, CF	SF, CF	W4, W3	W4	W1	W1, W2
Canopy height (m)	20.08	11.30	2.47	3.93	15.44	11.17	10.79	7.06
SD	±4.76	±4.75	±2.69	±6.77	±7.22	±8.17	±9.45	±6.49
<i>P</i> < 0.05	PA, LV, SF	PA, LV, CF	SF, CF	SF, CF	W4, W2, W3	W4, W1	W1	W1, W2
Slope (°)	33.66	29.13	26.93	20.40	32.61	32.67	24.67	24.99
SD	±9.29	±10.05	±11.77	±7.56	±9.48	±9.97	±8.53	±11.89
<i>P</i> < 0.05	PA, LV, SF	PA, CF	PA, CF	LV, SF, CF	W4, W3	W4, W3	W1, W2	W1, W2

CF, cloud forest; SF, secondary forest; LV, low vegetation; PA, pasture.

Table 3 Comparison of the actual number of traps used (left) and the number expected (right) if sampling had been perfectly proportional to the area of each vegetation type in each window and the types of vegetation on the landscape. In both cases, the goodness-of-fit analysis revealed that the number of traps used for the sampling did not differ significantly from expected. When expected values < 5 Fisher’s exact test was used. For the other cases, we calculated χ^2 . Windows (W) are listed in order of greatest to least cloud forest cover.

Vegetation type	Windows				χ^2_3	Landscape
	W1	W2	W3	W4		
Cloud forest	45/45	21/20	16/16	7/2	<i>P</i> > 0.48	89/83
Secondary forest	19/20	24/31	22/24	32/35	<i>P</i> > 0.95	97/110
Low vegetation	8/6	20/19	13/8	16/19	<i>P</i> > 0.67	57/52
Pasture	0/1	7/2	21/24	17/16	<i>P</i> > 0.26	45/43
χ^2_3	<i>P</i> > 0.9	<i>P</i> > 0.29	<i>P</i> > 0.68	<i>P</i> > 0.39		<i>P</i> > 0.72

Table 4 Multiplicative diversity partition for windows (W) and vegetation types (VT). Windows are listed in order of greatest to least cloud forest cover. Gamma diversity (γ), mean alpha diversity ($\bar{\alpha}$), and beta diversity (β) for richness (0D) and Shannon diversity (1D) are shown for W and VT.

Vegetation type	Windows				$\gamma_{VT} \ ^0D/^1D$	$\bar{\alpha}_{VT} \ ^0D/^1D$	$\beta_{VT} \ ^0D/^1D$
	W1 $^0D/^1D$	W2 $^0D/^1D$	W3 $^0D/^1D$	W4 $^0D/^1D$			
Cloud forest	10/3.53	10/3.85	10/3.94	4/3.38	13/4.38	8.5/3.79	1.53/1.15
Secondary forest	7/4.16	13/5.54	15/5.04	12/4.86	20/6.33	11.7/5.05	1.70/1.25
Low vegetation	7/5.53	12/6.95	13/5.56	8/5.05	17/8.23	10/5.91	1.70/1.39
Pasture		9/6.56	12/3.92	9/5.51	17/5.02	10/4.26	1.70/1.18
γ_w	10/4.27	16/5.86	18/5.81	15/6.50			
$\bar{\alpha}_w$	8/3.82	11/5.18	12.5/4.25	8.75/4.91			
β_w	1.25/1.12	1.45/1.13	1.44/1.32	1.71/1.32			

We calculated two measures of diversity: species richness and Shannon diversity. Both are part of the so-called true diversities qD , which obey the replication principle (Jost, 2007; Tuomisto, 2010). Species richness is diversity of the order $q = 0$, while Shannon diversity is of the order $q = 1$, which is the numbers equivalent of Shannon’s index. The numbers equivalent of a diversity index is the number of equally likely

species needed to produce the given value of the diversity index (Jost *et al.*, 2010); in this case, it is the exponential of Shannon’s index. Species richness (0D) is not sensitive to frequency and so gives disproportionate weight to rare species (Jost, 2006; Tuomisto, 2010). In contrast, Shannon diversity (1D) weights each species according to its frequency in the community, without favouring rare or abundant species (Jost,

2007). Similarly, 0D and 1D are the only measures of true diversity that can be partitioned into independent alpha and beta diversities when the weights of the communities are not equal (for all other values of q , alpha diversity can be greater than gamma diversity), something that normally applies to real data (Jost, 2007). Jost (2007) defines true beta diversity as the effective number of different communities in a given landscape or region, stating that the unequal sizes of the different communities play an essential role in the outcome; for a given set of distinct communities, beta diversity is smallest when one community dominates the landscape (minimal species turnover between sampling units) and is largest when all communities share the landscape equally (maximum species turnover; Jost, 2007).

To partition species richness into true alpha and beta diversities, we used the following formulas:

$${}^0D_Y = S$$

$${}^0D_\alpha = (1/N)(S_1 + S_2 + \dots + S_j)$$

$${}^0D_\beta = {}^0D_Y / {}^0D_\alpha,$$

where S_j is the number of species per sampling unit and N is the number of sampling units. 0D_Y is the total number of species in the entire set of sampling units.

To partition Shannon diversity into true alpha and beta diversities, we used the following formulas (Jost, 2007):

$${}^1D_Y = \exp \left[\sum_{n=1}^S (p_i \ln p_i) \right]$$

$${}^1D_\alpha = \exp \left[-w_1 \sum_{n=1}^S (p_{i1} \ln p_{i1}) + -w_2 \sum_{n=1}^S (p_{i2} \ln p_{i2}) + \dots \right]$$

$$w_j = \text{ind}_j / \text{ind}_{\text{TOT}}$$

$${}^1D_\beta = {}^1D_Y / {}^1D_\alpha,$$

where w is the statistical weight contributed by each sampling unit to the total diversity (number of individuals in community j divided by the total number of individuals).

We partitioned diversity on two scales: (1) Landscape gamma diversity into average alpha window diversity and the beta diversity between windows (spatial approach), and landscape gamma diversity into average alpha diversity of vegetation types and beta diversity between vegetation types (structural approach) and (2) We further partitioned each window and each vegetation type into their respective average alpha and beta diversities (Table 4).

Species grouping

We grouped the species in two ways (Table 5). The first was according to the biogeographical distribution patterns (BDP) proposed by Halffter (1976, 1978, 1987) for the MTZ that apply to the study region: Mesoamerican Montane (MAM), Typical Neotropical (TNT) and Tropical Palaeoamerican (TPA). These distribution patterns have been used to

understand the origin and integration of the insects in the MTZ and assume that there is a common history of colonization or speciation in each pattern. We used a χ^2 -test to detect whether relative frequencies of BDP for species and individuals were different between windows or vegetation types. Two species (0.5% of all individuals) did not fall into any of the distribution patterns and were excluded from the analysis (Table 5). The second grouping divides the community into species typical of CF (tCF-species, species that in addition to being captured in our CF have been reported in other studies) and atypical species that have not been reported for any CF in the region or are vagrant species (nCF-species, Table 5).

RESULTS

In total, we collected 4247 individuals belonging to 23 species (Table 5 includes nomenclatural authorities for all species). The estimators suggest that more than 90% of the species inhabiting the landscape were captured. The mean estimate was 89.6% (min. 71%, max. 100%) for windows and 87% (min. 73%, max. 100%) for vegetation types (Fig. 2). In CF and pastures, the estimators were over 87%, while in SF and low vegetation, the estimators were lower and more variable, indicating that between 73% and 94% of the predicted number of species were caught. Within each window, CF was the vegetation type with the greatest sampling efficiency.

For the vegetation types, richness was lowest in CF (13 species) and highest in SF (20 species). Windows richness varied from 10 (W1) to 18 species (W3). The richness of W1 and CF was significantly lower than that of a sample taken randomly from the entire landscape (Fig. 2), while there were no significant differences in the other windows or vegetation types (i.e. their values fall within the 95% confidence intervals). Within each window, the SF and low vegetation, and even some pastures (in W3 and W4) were richer in species than CF was, with the exception of W1 where richness was greater in CF, and the richness of SF and LV was an impoverished subset of that of CF (Table 4).

Shannon diversity was lowest in W1 which is dominated by CF and highest in W4 which has less CF. As the less diverse vegetation type, the diversity of CF was 50% lower than that of the low vegetation. In the windows, CF consistently had the lowest Shannon diversity values (Table 4).

Diversity partitioning

The greater relative importance of alpha diversity and the lower contribution of beta diversity were reflected in the partition for both vegetation types (${}^0D_{VT}$: 23 = 16.75 × 1.37; ${}^1D_{VT}$: 7.13 = 5.55 × 1.28) and windows (0D_W : 23 = 14.75 × 1.56; 1D_W : 7.13 = 5.69 × 1.25). This pattern was also observed inside the windows, though with greater variation in the contribution of alpha and beta (Table 4). The beta diversity of the two measures exhibited a clear pattern: as the degree of modification within the window increases so does beta diversity (Table 4).

Table 5 Dung beetle species abundance in the cloud forest landscape with the species sorted by their abundance in CF.

	BDP	ACF	CF	SF	LV	PA	W1	W2	W3	W4	LS
<i>Deltochilum mexicanum</i> Burmeister 1848	MAM	tCF	681	417	101	33	241	414	517	60	1232
<i>Dichotomius satanas</i> Harold 1867	TNT	tCF	225	455	155	387	40	132	872	178	1222
<i>Ontherus mexicanus</i> Harold 1868	MAM	tCF	99	226	43	49	5	226	123	63	417
<i>Onthophagus</i> , sp. nov. aff. <i>belorhinus</i>	MAM	tCF	74	156	26	14	101	18	58	93	270
<i>Eurysternus magnus</i> Castelnau 1840	MAM	tCF	37	41	49	13	19	64	52	5	140
<i>Canthidium ardens</i> Bates 1887	TNT	tCF	35	132	15	2	73	27	83	1	184
<i>Onthophagus cyanellus</i> Bates 1868	MAM	tCF	35	17	14			66			66
<i>Onthophagus incensus</i> Say 1835	TPA	tCF	15	47	28	300	7	17	343	23	390
<i>Coprophanaeus gilli</i> Arnaud 1997	TNT	tCF	10	4	2		2	6	7	1	16
<i>Copris incertus</i> Say 1835	TPA	tCF	8	21	13	166	2	4	170	32	208
<i>Phanaeus amethystinus</i> Harold 1863	MAM	tCF	3	1		2		6			6
<i>Canthidium pseudoperceptibile</i> Kohlmann & Solis 2006	TNT	tCF	2	3	11	1	1	13	3		17
<i>Coprophanaeus corythus</i> Harold 1863	TNT	tCF	1	4	1	4		2	5	3	10
<i>Onthophagus subcancer</i> Howden 1973	MAM	tCF*	1	1	2			2	1		3
<i>Onthophagus durangoensis</i> Balthasar 1939	-	nCF	2	2	14	3		8	3	8	19
<i>Phanaeus sallei</i> Harold 1863	TNT	nCF	1	1		16				17	17
<i>Onthophagus nasicornis</i> Harold 1869	TPA	nCF			8	4			11	1	12
<i>Dichotomius colonicus</i> Say 1835	TNT	nCF			1	8			9		9
<i>Copris laeviceps</i> Harold 1869	TPA	nCF		3		1			1	3	4
<i>Onthophagus igualensis</i> Bates 1886	-	nCF		1	1				2		2
<i>Ateuchus illaesum</i> Harold 1868	TNT	nCF		1				1			1
<i>Canthon cyanellus</i> LeConte 1859	TNT	nCF				1				1	1
<i>Uroxys boneti</i> Pereira & Halfiter 1961	TNT	nCF		1					1		1
∑ individuals			1225	1534	484	1004	491	1006	2261	489	4247
Number of individuals of CF species as a % of all the individuals in VT or W			100	99.4	95.0	96.7	100	99.1	98.8	93.9	98.4
Ind/trap†			13.8 LV	16.0 LV	8.2 CF,SE,PA	22.8 LV	6.8 2,3	14.0 1,3,4	31.4 1,2,4	6.8 2,3	14.7
Biomass/trap† (mg)			3563 LV	3599 LV	1820 CF,SE,PA	4158 LV	1251 2,3	3074 1,3,4	7428 1,2,4	1482 2,3	3309
Biomass/ind/trap† (mg)			250 PA,LV	216	213 CF	186 CF	190 3	220	246 1	228	221

*The inclusion of *O. subcancer* is based on our preliminary sampling of 2007 and the results of other studies.

†Differences among sampling units (between vegetation types CF, SF, LV, PA; between windows 1, 2, 3, 4) were calculated using a Kruskal–Wallis test ($P < 0.05$).

CF, cloud forest; SF, secondary forest; LV, low vegetation; PA, pasture; BDP, biogeographical distribution patterns; MAM, mesoamerican montane; TNT, typical Neotropical; TPA, Tropical Palaeoamerican; ACF, affinity to cloud forest; tCF, typical cloud forest species; nCF, not typically cloud forest species.

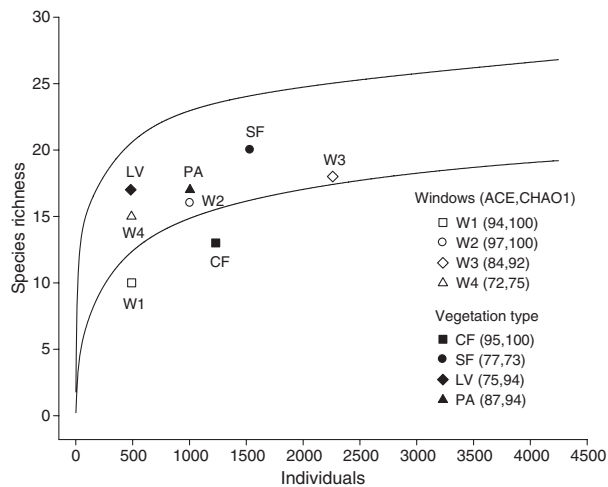


Figure 2 Lower and upper boundaries of the 95% confidence intervals for the landscape richness of dung beetles and the observed richness for the Windows (W) and vegetation types (VT). Points within the limits of the confidence interval do not differ significantly from a sample of the same number of individuals taken randomly from the whole landscape. Percentage observed richness and expected richness (ACE and CHAO1 estimators) are given in parenthesis. CF, cloud forest; SF, secondary forest; LV, low vegetation; PA, pasture.

In terms of vegetation type, CF had the lowest diversity values for both richness and Shannon diversity. While the transformed vegetation types had similar richness values, for Shannon diversity, the low vegetation had the highest alpha and beta values, followed by SF and pasture, the latter differing little from CF (Table 4).

In all cases, the expression of Shannon beta diversity was lower than the beta from species richness, indicating that the differences between the sampling units result more from rare species, while the abundant species are the same (Tables 4 and 5).

Abundance and biomass

We found differences in dung beetle abundance and biomass between windows and between vegetation types (Table 5). Abundance in W3 was four times greater than in the two windows with the lowest abundance (W1 and W4). Low vegetation (LV) had the fewest individuals per trap, and pasture was the vegetation type with the greatest number of individuals per trap. The pattern was the same for biomass per trap (BT), but not for individual biomass per trap (IBT) where CF had the highest and pasture the lowest biomass. Although the frequency of small individuals increased with the degree of habitat transformation, the beetles belonging to large species and with a high biomass dominated in all the sampling units (Table 5).

Ecological and biogeographical distribution pattern

There are a total of 14 species on our landscape that are typical of CF. Individuals of tCF-species dominated the landscape, the

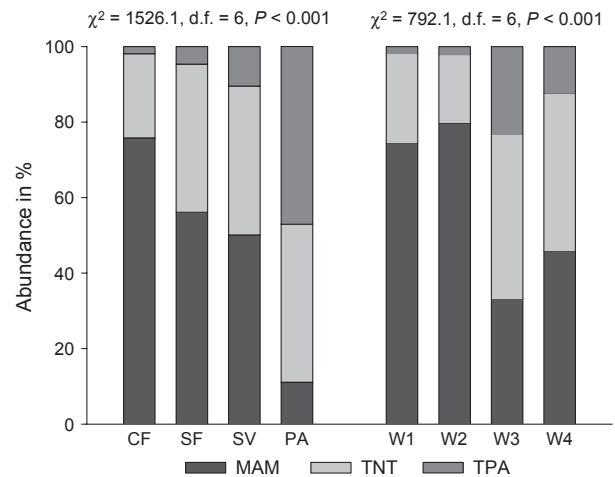


Figure 3 Proportion of individuals belonging to species with the following biogeographical distribution patterns. MAM, Meso-american Montane; TNT, typical Neotropical; TPA, Tropical Palaeoamerican; CF, cloud forest; SF, secondary forest; LV, low vegetation; PA, pasture. Windows are listed in order of greatest to least cloud forest cover. For vegetation types: $\chi^2_{\text{TPA}} = 972.2^{***}$, $\chi^2_{\text{MAM}} = 473.2^{***}$, $\chi^2_{\text{TNT}} = 80.7^{***}$; for windows: $\chi^2_{\text{MAM}} = 359.7^{***}$, $\chi^2_{\text{TPA}} = 280.9^{***}$, $\chi^2_{\text{TNT}} = 151.6^{***}$ (***) d.f. = 3, $P < 0.001$).

windows and vegetation types, contributing more than 90% in each sampling unit (Table 5). Of the total number of species collected (23), eight species were found in all of the windows and all vegetation types and were the most abundant. Two species with more than one individual captured – *Onthophagus cyanellus* (locally abundant) and *Phanaeus amethystinus* (a rare species) – were only found in one of the windows. Of the species found in CF (13), three were collected in three vegetation types and the other ten in all of the vegetation types. The three species that were most abundant in pasture (*Dichotomius satanas*, *Onthophagus incensus* and *Copris incertus*) were also present in CF, with *D. satanas* occupying second place in CF in terms of abundance (Table 5) and biomass (see Table S1 in Supporting Information).

Although there was not much difference between sampling units in the number of species according to their biogeographical distribution (Table 5), the differences in abundance were highly significant for all sampling units (Fig. 3). Based on the number of individuals, species with the MAM pattern dominated three of the four vegetation types (not pasture) and two of the windows (W1 and W2), and even though W2 has less CF than W1, its percentage of dung beetles with the MAM pattern was greater. The pastures were dominated by individuals belonging to species with the Tropical Palaeoamerican pattern. Individuals with the Neotropical pattern dominated two windows (W4 and W3), but did not dominate any of the vegetation types (Fig. 3). The contribution of dung beetles with the Tropical Palaeoamerican pattern in the vegetation types increased with increasing modification.

DISCUSSION

In the variegated landscape we studied, the transformation of CF contributes to an increase in species richness on the landscape and thus corroborates the results of other authors for different regions in tropical America (Arellano & Halffter, 2003; Escobar, 2004; Halffter *et al.*, 2009; Horgan, 2009). CF had a less diverse dung beetle fauna than the other types of modified vegetation, although it was the best sampled vegetation type according to the estimators. In addition to low richness, the low value for Shannon diversity in CF resulted from the dominance of *Deltochilum mexicanum*.

Modified vegetation types had a more diverse dung beetle fauna for two reasons: (1) the typical CF species were present in these modified vegetation types and (2) new species that are mainly found at lower altitudes managed to make it up to the landscape and survive there. Therefore, the transformed vegetation types are permeable to tropical forest species from the lowlands, but the CF is not. We interpret the values of the ACE and CHAO1 estimators for the transformed vegetation types and windows as a high temporal turnover of rare species, rather than as a lack of adequate sampling (Fig. 2). Although the species not present in CF increased the richness of the landscape by $\approx 40\%$, they contributed $< 1.6\%$ to total abundance and $< 0.5\%$ to total biomass. This allows us to posit that we are dealing with occasional penetrations that do not form permanent populations; species whose entry into the landscape was favoured by its variegated structure. Species such as *Ateuchus illaesum*, *Uroxys boneti*, *Copris laeviceps*, *Phanaeus sallei* and *Canthon cyanellus* – rare in our samples – are common or abundant in the tropical forests of the lowlands (Edmonds, 1994; Navarrete & Halffter, 2008; Díaz *et al.*, 2010).

The 14 species typical of CF form two different groups. The first group has most of its distribution in the CF and are species with the MAM distribution pattern plus *Coprophanaeus gilli* (Edmonds & Zidek, 2010). These species are not necessarily more abundant in the forest (Table 5). The only species that is clearly affected by the modification of the CF and whose abundance decreases without disappearing from any of the modified vegetation types is *D. mexicanum*. The other species typical of CF either have a greater number of individuals per trap in the other vegetation types (e.g. *Eurysternus magnus*) or exhibit no clear tendencies. The only rare species that is typical of CF is *P. amethystinus* (Edmonds, 1994). The other group includes species typical of the CF community (not necessarily abundant), but widely distributed in other tropical forests in the MTZ. The most significant of these are *D. satanas*, *C. incertus* and *O. incensus* (Matthews, 1961; Kohlmann, 2003). These three species were reported in the CF in all of the studies carried out in adjacent regions, but are frequently more abundant in transformed types of vegetation (Arellano & Halffter, 2003; Arellano *et al.*, 2004; Pineda *et al.*, 2005; Halffter *et al.*, 2009).

With respect to biomass, in contrast to that reported by Nichols *et al.* (2007) and Gardner *et al.* (2008), on our landscape, one high biomass species (*D. mexicanum*) is

replaced by another (*D. satanas*) with the modification of the habitat. We did not observe that large species tend to disappear and be replaced by small species as indicated for modified tropical forests (see Table S1). Whether our observation is because of local characteristics, general differences between mountain and lowland landscapes, or between ecosystems in the MTZ and South America, will have to be addressed in future studies.

Comparison of communities with different biogeographical histories

The results presented here (Fig. 3, Table 5) are determined by the biogeographical history of the MTZ (Halffter, 1976), because similar patterns have been reported for the Scarabaeinae of other landscapes in the MTZ (Arellano & Halffter, 2003; Pineda *et al.*, 2005; Escobar *et al.*, 2007; Halffter *et al.*, 2009). The opposite was found in ecologically analogous landscapes outside of the MTZ. From a landscape in the Colombian Andes, Escobar (2004) collected a total of 20 species, 12 of them in CF, numbers quite similar to ours. However, there is a big difference in dung beetle composition and abundance in the strongly modified vegetation types. For cropland, 99.8% of the individuals belonged to species not present in CF (in our study, this number was never $> 5\%$ for any type of vegetation), and these species accounted for more than 50% of the landscape's total abundance.

The species with a Tropical Palaeoamerican pattern, which increased in abundance at more transformed sites at the expense of species with a MAM pattern, are only slightly represented in South America. Thus, there are relatively few species of *Onthophagus* in South America (Zunino & Halffter, 1997; Escobar *et al.*, 2007) and only one species of *Copris* (Matthews, 1961). Escobar *et al.* (2007) observed that along an altitudinal gradient in Mexico, there were no differences in richness or abundance between forests and pastures, while in the Colombian Andes, the forest was richer in species at all altitudinal levels. The majority of the lineages of Neotropical origin have a strong affinity for forests and therefore are affected by the modification of this habitat type. In contrast, among the lineages of northern origin (the Palaeoamerican pattern), many species are adapted to living in sunny conditions. This explains the importance of these lineages in the modified vegetation types of our landscape.

Landscape variegation model and sampling design

As expected for a variegated landscape, the species of the CF community move throughout the entire landscape and in consequence, beta diversity is relatively low. Nevertheless, there are differences in the community response depending on the degree of modification: the more modified a window, the greater the beta diversity is (Table 4). However, even in the fragmented windows (W3 and W4), beta diversity is not high, because CF and SF combined cover more than 50% of the total area. Apart

from our study and some others (e.g. Lindenmayer *et al.*, 2003), there is little empirical support for continuous landscape models (Price *et al.*, 2009). Thus, it is interesting that the results correspond to those of a variegated landscape. The limits that differentiate variegated landscapes from fragmented (10–60% of original habitat) or intact ones (> 90% of original habitat) are based on theoretical studies (Pearson *et al.*, 1996). The spatial arrangement of the vegetation types is expected to play an equally important role. Escobar (2004) states that in a landscape with > 60% CF, he collected dung beetle communities that were totally different in CF and cropland (equivalent to the low vegetation of our landscape). One reason could be that the different types of vegetation on the landscape studied by Escobar are spatially distributed in a compact manner with large areas and well-defined edges. Consequently, the landscape studied by Escobar (2004), although variegated because of the proportion of original habitat, is actually a fragmented landscape given the arrangement of its elements, as shown by the response of the Scarabaeinae community. The array of different vegetation types appears to have a notable influence on the possibility of the biota of the original forest surviving in the transformed vegetation types, and the variegated landscape favours the persistence of the dung beetle species that inhabited the original vegetation.

Gardner *et al.* (2008) emphasize that many studies do not take into account possible sampling bias resulting from spill over and edge effects, spatial pseudoreplication and insufficient replication. They minimized confounding edge and fragmentation effects on a landscape in the north-eastern Brazilian Amazon, with long tracts of continuous rain forest habitat, SF and eucalyptus plantations. We think that their conclusions are valid for landscapes or regions similar to the one they studied, but not in general for other types of transformed tropical landscapes that are mainly in the mountains. There are many human-modified landscapes with both gradual and continuous changes in the vegetation, in different stages of modification, highly heterogeneous and with countless spatial arrays (Feinsinger, 1994; Greenberg, 1996; Nepstad *et al.*, 1996; McIntyre, 2007), just like the landscape we studied. In these variegated landscapes, there are edges everywhere (Feinsinger, 1994) and they cannot and should not be excluded from sampling. A random or semi-random sampling design may be adequate to include edges according to their impact and abundance in the landscape.

The value of transformed habitats for species conservation

Recently, there has been a lot of controversy about the value of SFs and other systems that are modified versions of the original vegetation for the conservation of biodiversity (Dunn, 2004; Brook *et al.*, 2006; Wright & Muller-Landau, 2006a,b; Barlow *et al.*, 2007; Gardner *et al.*, 2007) including that of dung beetles (Quintero & Roslin, 2005; Nichols *et al.*, 2007; Gardner *et al.*, 2008), with strong arguments for and against. The biogeographical affinities in the region and the type of landscape may be determining factors for the value of modified vegetation

types for dung beetle conservation. Mountainous tropical landscapes appear to differ markedly from lowland tropical landscapes, so they should only be compared with caution. Mountainous landscapes extend along very narrow vertical strips that are often in contact with very different ecosystems where the communities have different biogeographical or ecological histories. Here, one consequence of habitat modification is the invasion of species from higher altitudes (rare cases) or from lower down (e.g. Halffter *et al.*, 1995; Escobar, 2004). In flat areas such as the region studied by Gardner *et al.* (2008) where there are no marked changes in the climate or in the biogeographical history over large distances, the number of invaders is relatively low. Tropical mountain ecosystems have a high degree of natural disturbances; their typical species are expected to have adapted to these dynamic conditions and exhibit ecological behaviour sufficiently robust, so that they might be less affected by anthropogenic disturbances. In landscapes with a lower degree of natural disturbances, the susceptibility of species to anthropogenic disturbances could be much greater.

Current anthropogenic land use in our landscape is not having an evident negative effect on Scarabaeinae diversity. Future management should aim to achieve two main goals: to protect the CF areas, even the small ones, and to promote land use that includes arboreal cover, rather than leaving large, treeless tracts. Maintaining the variegated character of the landscape or transforming fragmented landscapes into variegated ones could be a conservation goal (Manning *et al.*, 2004; Fischer & Lindenmayer, 2006) that would apply to several mountainous tropical landscapes, especially in the MTZ.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Dung beetle species biomass in the cloud forest landscape.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

Matthias Rös' research focuses on patterns of dung beetle diversity in natural and human-modified landscapes, the processes that generate them and the implications for conservation.

Federico Escobar has worked for the past 18 years on patterns in the diversity of dung beetles in the Neotropics. He is interested in how human activities influence spatial heterogeneity and how this can be applied to decision-making in conservation.

Gonzalo Halffter is one of the world's leading specialists in the ecology, biology and ethology of dung beetles, and has published two seminal studies (one with Eric Matthews, the other with David Edmonds) in addition to many chapters and scientific papers on the subject. Biogeography and the biodiversity of Mexico are also strong areas of interest, and he has written extensively about biosphere reserves and their importance to the conservation of native biota.

Author contributions: M.R., F.E. and G.H. planned all aspects of the field work. M.R. collected and analysed the data, and wrote the manuscript. All of the authors made substantial contributions to the final document.

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